ABUNDANCE, BIOMASS AND ESTIMATED PRODUCTION OF INVERTEBRATE FAUNA ASSOCIATED WITH SEAGRASS, *HETEROZOSTERA TASMANICA*, IN SWAN BAY AND AN ADJACENT AREA OF PORT PHILLIP BAY, VICTORIA

FIONA L. BIRD[1,2] & GREGORY P. JENKINS[1]

[1] Marine and Freshwater Research Institute, and Zoology Department, University of Melbourne,
PO Box 138, Queenscliff, Victoria 3225, Australia
[2] Present address: Crustacea laboratory, Museum of Victoria, 71 Victoria Cresent, Abbotsford,
Victoria 3067, Australia

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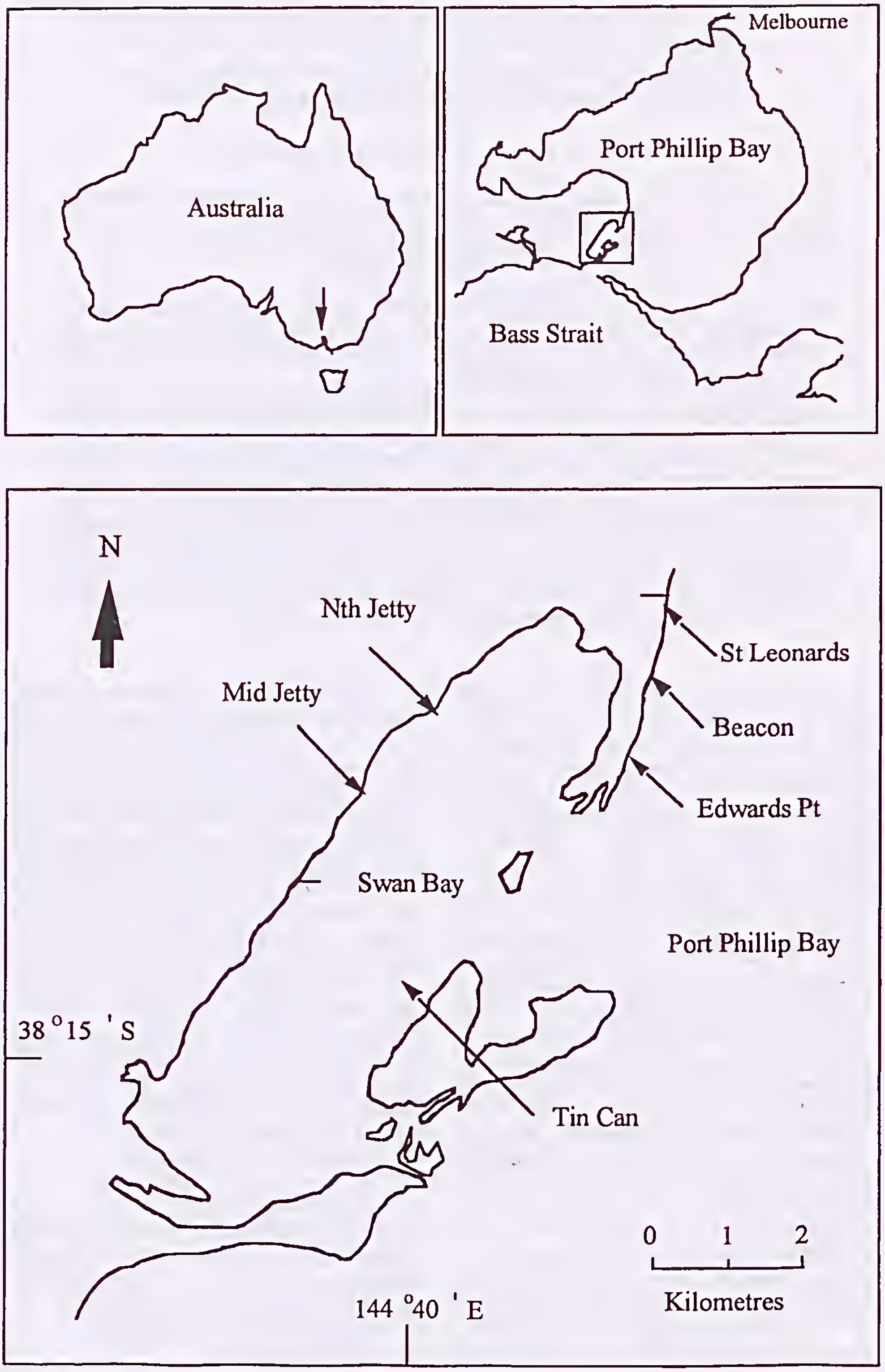
Abundance, biomass and production of invertebrates were compared between Swan Bay, a seagrass system in a low energy sheltered environment, and an adjacent area of Port Phillip Bay, which had greater exposure to wave action and tidal currents. Seagrass biomass and abundances of macrofauna were not significantly different between the two areas, but organic content of sediments, biomass and production of macrofauna were significantly higher in Swan Bay. Faunal composition was markedly different, with Port Phillip Bay sites dominated by gammaridean and caprellidean amphipods, while a variety of often larger macrofaunal groups characterised Swan Bay sites. In contrast to macrofauna, the epibenthic meiofauna, dominated by harpacticoid copepods, was significantly more abundant in Swan Bay. The results support the contention that sheltered seagrass areas with elevated organic content of sediment can provide increased production of food for juvenile fish.

SEAGRASS beds are known to be highly productive environments (Hillman et al. 1989), supporting diverse and extensive communities of invertebrates. Studies comparing seagrass and unvegetated habitats have consistently found that vegetated areas sustain greater abundance and diversity of benthic invertebrates (Rainer & Fitzhardinge 1981; Poore 1982; Lewis 1984; Howard et al. 1989; Edgar 1990a) and fish (Bell & Pollard 1989; Lubbers et al. 1990; Blaber et al. 1992). Seagrass is known to trap organic debris and detritus (Norwell & Jumars 1984), with the organic material thought to enhance the secondary production (Pearson & Rosenberg 1978; Mann 1988; Spies et al. 1988). From this observation it is hypothesised that exposed habitats accumulate less detritus than sheltered habitats and would consequently have lower overall production levels. Edgar (1990a) showed by comparing a sheltered to an exposed area, that organic enrichment of sediments (by debris and detritus) enhances invertebrate production.

Swan Bay, Australia, has extensive beds of the subtidal seagrass, *Heterozostera tasmanica*, in a low energy, sheltered environment with large accumulations of debris and drift algae. The adjacent coast of Port Phillip Bay has smaller, more discrete *H. tasmanica* beds in a higher energy environment with less accumulated debris. This area of Port Phillip Bay is adjacent to strong tidal currents associated with exchange of water through the narrow entrance at Port Phillip Heads (Black et al. 1993). Shaw & Jenkins (1992) showed that unvegetated areas of Swan Bay had finer sediments with higher organic content than unvegetated areas of the adjacent coast of Port Phillip Bay. Jenkins et al. (in review) found that fish communities in these seagrass beds were dominated by juveniles, and the abundance and biomass of fishes in Swan Bay was significantly higher than in the adjacent coast of Port Phillip Bay. Juvenile fishes at these sites consumed small invertebrates, dominated by Crustacea (Bird 1990). Edgar & Shaw (1993) found that fish and invertebrate production in Western Australia was much higher in sheltered than in exposed sites, and postulated that fishes were attracted to seagrass beds with high production of invertebrates. We postulated that the more sheltered environment of Swan Bay would result in correspondingly higher organic content of sediments and elevated production of invertebrates. In this paper, we examine this hypothesis by comparing organic content of sediments, meiofauna abundance, and macrofaunal abundance, biomass and production in Swan Bay and an adjacent area of Port Phillip Bay.


Australia
Melbourne
Port Phillip Bay
Bass Strait
N
Nth Jetty
Mid Jetty
St Leonards
Beacon
Edwards Pt
Swan Bay
Port Phillip Bay
38 °15 ' S
Tin Can
0 1 2
Kilometres
144 °40 ' E

METHODS

Study area

The study area included Swan Bay and an adjacent area in Port Phillip Bay, situated on the Bellarine Peninsula, Victoria (Fig. 1). Tidal currents in Swan Bay are less than 0.05 ms^{-1} compared with currents between 0.1 and 0.5 ms^{-1} on the adjacent coast of Port Phillip Bay (Black et al. 1993). Moreover, maximum wind fetch is less than 10 km in Swan Bay, but greater than 40 km on the adjacent coast of Port Phillip Bay (Fig. 1). Two sites were sampled in Swan Bay; Tin Can and North Jetty, and two sites were sampled in Port Phillip Bay; St Leonards and Beacon. Samples were taken seasonally over two days beginning on 1 May, 1 August, 29 October 1990 and 20 January 1991. One additional site in each area, Mid Jetty and Edwards Point, was included in October for sampling of organic content of sediment and meiofauna abundance (Fig. 1).

Field methods

The invertebrate community was sampled using two sizes of corers. A 90 mm diameter PVC core, was used to take five haphazardly placed replicates, from each of the four sites on all four dates, to estimate abundance, biomass and production of macrofauna. A 32 mm diameter corer was used to obtain eight replicate samples at each of the six sites in October. Five replicates from each site were used for analysis of organic content and the remaining three for analysis of meiofauna. Both of the corers were pushed into the sediment to a depth of 10 cm to extract a constant volume of sediment. The samples were preserved in 99% ethanol mixed with Rose Bengal to make the animals more visible while sorting.

Laboratory methods

Each large-core sample was washed through a series of nested sieves of 5.6, 4.0, 2.8, 2.0, 1.4, 1.0, 0.71 and 0.5 mm mesh. Small cores were washed through a sieve series of 0.5, 0.355, 0.25, 0.18, 0.125 and 0.063 mm mesh. Each category of invertebrate in each size class was counted. Seagrass biomass was estimated by drying the seagrass material remaining in the largest sieve for 48 hours at 60°C. Organic content of the sediment was estimated from the small-core samples. Total contents of each sample was dried for 48 hours at 60°C and then burned in a combustion oven for two hours at 500°C. The change in weight due to the burning was recorded, and this change was considered proportional to the organic content.

Data analysis

Analysis of macrofauna was restricted to invertebrates passing through the 5.6 mm sieve because larger animals were not consumed by juvenile fish in the study area (Bird 1990), and in the case of mobile animals, would have a greater ability to avoid the corer. Core data were initially checked for homogeneity of variances using Cochran's test, and if necessary log(x+1) or square-root transformed. The data were then analysed using an analysis of variance with two bays, two sites nested within each bay, five replicates at each site, on each of four dates. Time and bay were treated as fixed factors, while sites were considered to be random factors.

The biomass of macrofaunal groups was estimated from abundance and previously determined mean weights of these groups in individual sieve-size classes (Edgar 1990b). The production of a specific size-class and type of epifaunal invertebrate was calculated using the equation developed and tested by Edgar (1990b) which relates daily macrobenthic production (µg/d) to ash-free dry weight (µg) and water temperature (°C). The estimated production of a specific macrofaunal group in a given size class was multiplied by the number in that size class and summed for all size classes. Total daily production was estimated from the combined production values for each macrofaunal category.

RESULTS

Bay and site characteristics

Water temperatures tended to greater extremes in Swan Bay than in Port Phillip Bay (Table 1). Temperatures conform to those found by Jenkins (1986) except in October when we encountered an unseasonally warm sampling day. When

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Fig. 1. Location of the sampling sites in Swan Bay and an adjacent area of Port Phillip Bay.

calculating production estimates for that date, the temperature 170°C (from Jenkins 1986) was used for all sites. No significant difference in seagrass biomass was found between bays (Table 2). The seagrass biomass values ranged from 4 to 10 g per core (628 to 1572 g.m^{-2}) (Fig. 2). More detritus, seagrass debris and drift algae was observed inside Swan Bay than at the sites in Port Phillip Bay. Swan Bay sediment was shown to have a greater organic content than sediment in Port Phillip Bay (Table 3). A difference in organic content was also found between the Swan Bay sites (Fig. 3).

Sites	Date			
	May 1990	August 1990	October 1990	January 1991
North Jetty	15.5	12.1	25.0	22.3
Tin Can	14.7	10.9	25.0	21.4
St Leonards	16.4	11.5	18.9	20.2
Beacon	17.0	11.5	18.2	19.8

Table 1. Water temperature measurements taken at four sites in Swan Bay and an adjacent area of Port Phillip Bay (°C).

Source	Mean square	DF	F-ratio	P
Date	18.727	3	1.681	0.269
Bay	18.075	1	3.342	0.209
Date*Bay	9.902	3	0.889	0.499
SB sites	10.816	1	1.405	0.240
PPB sites	0.001	1	0.000	0.993
SB sites*Date	5.164	3	0.671	0.573
PPB sites*Date	17.123	3	2.225	0.094
Error	7.696	64		

Table 2. Nested analysis of variance comparing the estimated seagrass biomass in Swan Bay (SB) and an adjacent area of Port Phillip Bay (PPB). DF—degrees of freedom; P—probability.

Source	Mean square	DF	F-ratio	P
Bay	0.228	1	8.545	0.043
SB sites	0.051	2	7.385	0.005
PPB sites	0.002	2	0.306	0.741
Error	0.007	16		

Table 3. Nested analysis of variance comparing the organic content of sediments in Swan Bay (SB) and an adjacent area of Port Phillip Bay (PPB). DF—degrees of freedom; P—probability.

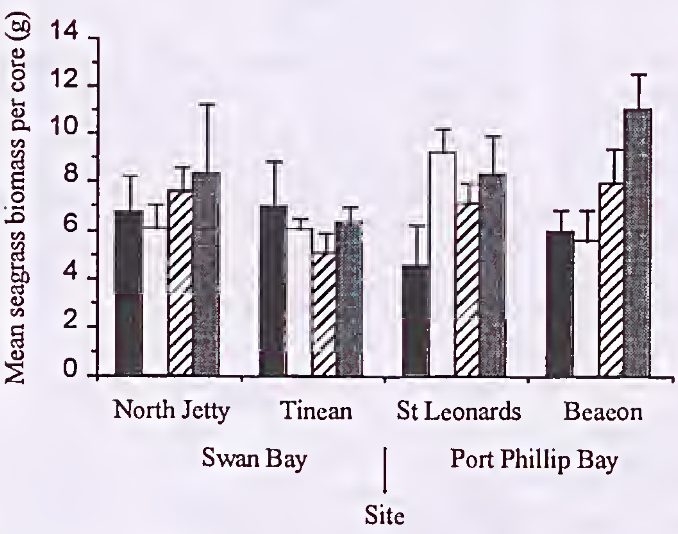

Fig. 2. Mean seagrass biomass at sites in Swan Bay and Port Phillip Bay on four sampling dates. Solid, 30 May 1990; open, 31 August 1990; diagonal, 30 October 1990; stipples, 31 January 1991. Error bars are standard error.

Macrofaunal communities

No significant difference in macrofaunal abundance was found between bays (Table 4, Fig. 4). Swan Bay had a significantly higher estimated biomass of macrofauna than Port Phillip Bay (Table 5). Macrofauna biomass also varied significantly amongst dates (Table 5). In general, biomass of macrofauna was highest for May and August samples in Swan Bay (Fig. 4). There was also a significant interaction between abundances at sites in Swan Bay with date (Table 5). Estimated production of macrofauna for Swan Bay was also significantly higher than for

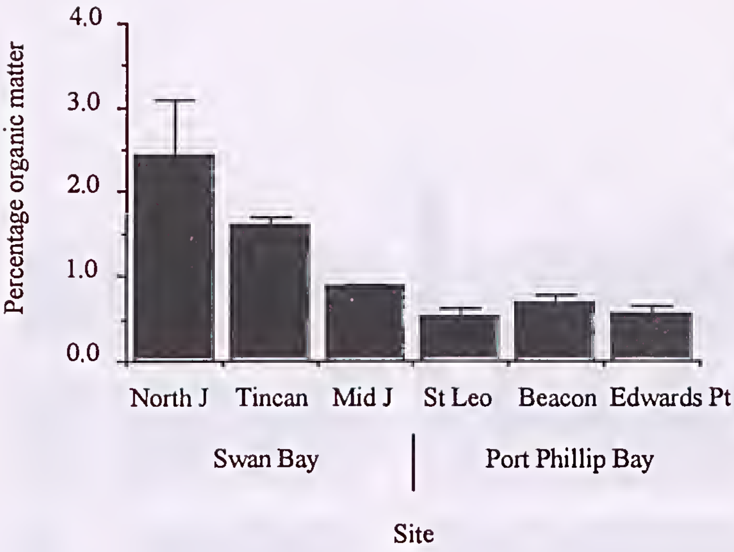

Fig. 3. Mean percentage of organic content in sediments at sites in Swan Bay and Port Phillip Bay. North J—North Jetty; Mid J—Mid Jetty; St Leo—St Leonards. Error bars are standard error.

Source	Mean square	DF	F-ratio	P
Date	19173.7	3	2.338	0.173
Bay	52173.1	1	5.600	0.142
Date*Bay	25052.4	3	3.055	0.113
SB sites	270.4	1	0.041	0.839
PPB sites	18361.2	1	2.814	0.098
SB sites*Date	14458.5	3	2.214	0.095
PPB sites*Date	1944.0	3	0.298	0.827
Error	6530.4	64		

Table 4. Nested analysis of variance comparing the abundance of macrofauna in Swan Bay (SB) and an adjacent area of Port Phillip Bay (PPB). DF—degrees of freedom; P—probability.

Source	Mean square	DF	F-ratio	P
Date	0.046	3	1.578	0.290
Bay	2.126	1	55.900	0.017
Date*Bay	0.093	3	3.204	0.105
SB sites	0.044	1	1.972	0.165
PPB sites	0.032	1	1.435	0.235
SB sites*Date	0.048	3	2.160	0.101
PPB sites*Date	0.010	3	0.432	0.731
Error	0.022	64		

Table 6. Nested analysis of variance comparing the estimated production of macrofauna in Swan Bay (SB) and an adjacent area of Port Phillip Bay (PPB). DF—degrees of freedom; P—probability.

Source	Mean square	DF	F-ratio	P
Date	9525.3	3	6.459	0.026
Bay	64412.6	1	104.515	0.009
Date*Bay	3381.5	3	2.293	0.178
SB sites	703.9	1	1.006	0.320
PPB sites	528.7	1	0.756	0.388
SB sites*Date	2640.9	3	3.774	0.015
PPB sites*Date	308.7	3	0.441	0.724
Error	699.7	64		

Table 5. Nested analysis of variance comparing the biomass of macrofauna in Swan Bay (SB) and an adjacent area of Port Phillip Bay (PPB). DF—degrees of freedom; P—probability.

Port Phillip Bay (Table 6). The highest estimated production of approximately 170 $mg.m^{-2}.d^{-1}$ was recorded at Tin Can in May (Fig. 4). Production estimates were also significantly different between sites in Swan Bay, however, this varied with date (Table 6). Annual production in $g.m^{-2}.yr^{-1}$ at each site was estimated to be 45.5 for North Jetty, 39.7 for Tin Can, 18.6 for St Leonards and 21.2 for Beacon.

Macrofaunal communities in seagrass beds were distinctly different between the two bays (Fig. 5). Amphipods dominated in Port Phillip Bay sites; caprellid amphipods were found only in Port Phillip Bay, and gammaridean amphipods were at

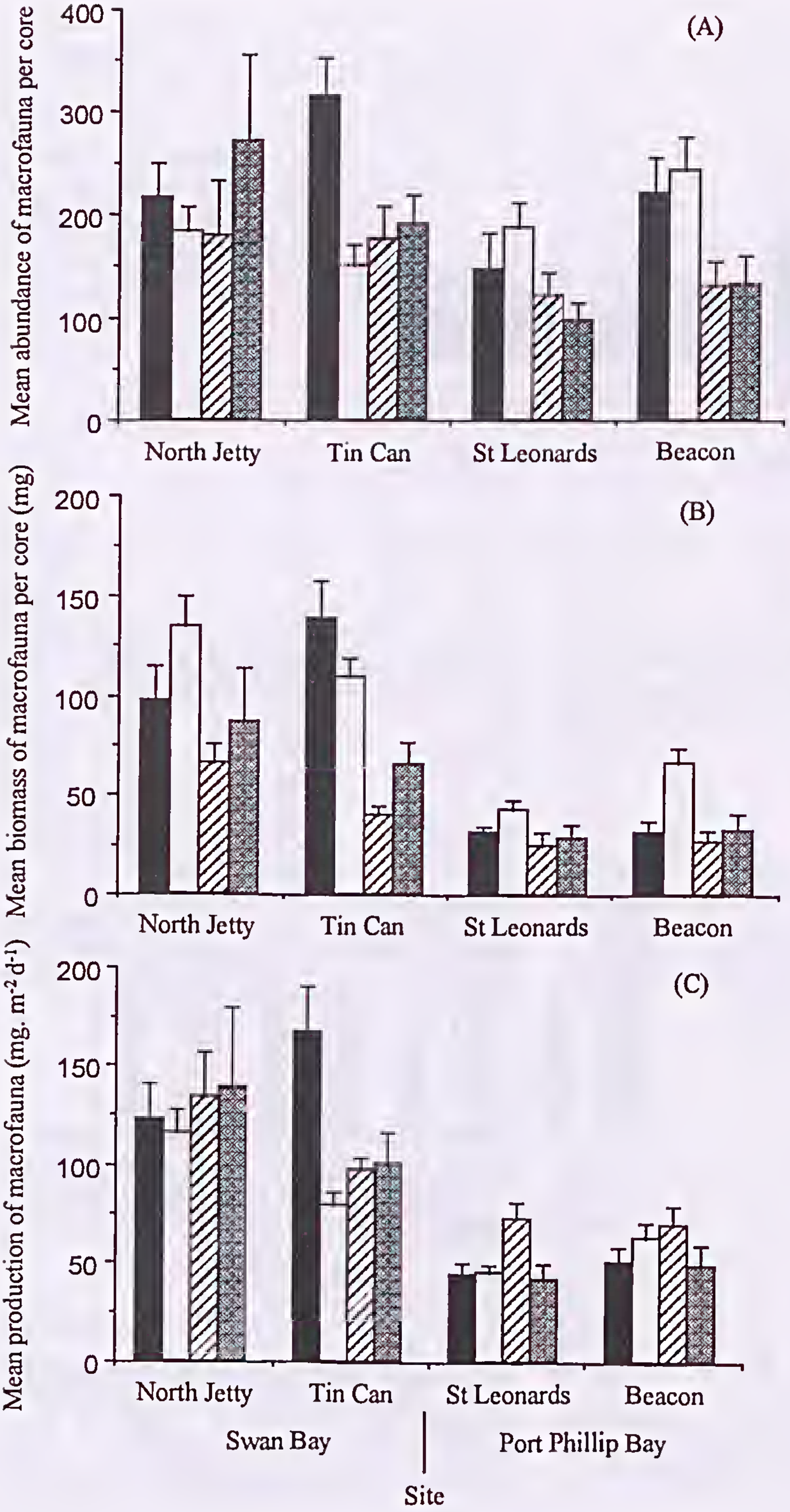

Fig. 4. Mean abundance, biomass, and estimated production of macrofauna at sites in Swan Bay and Port Phillip Bay on four sampling dates:
(A) abundance;
(B) biomass;
(C) production.
Key to dates in caption for Fig. 2. Error bars are standard error.

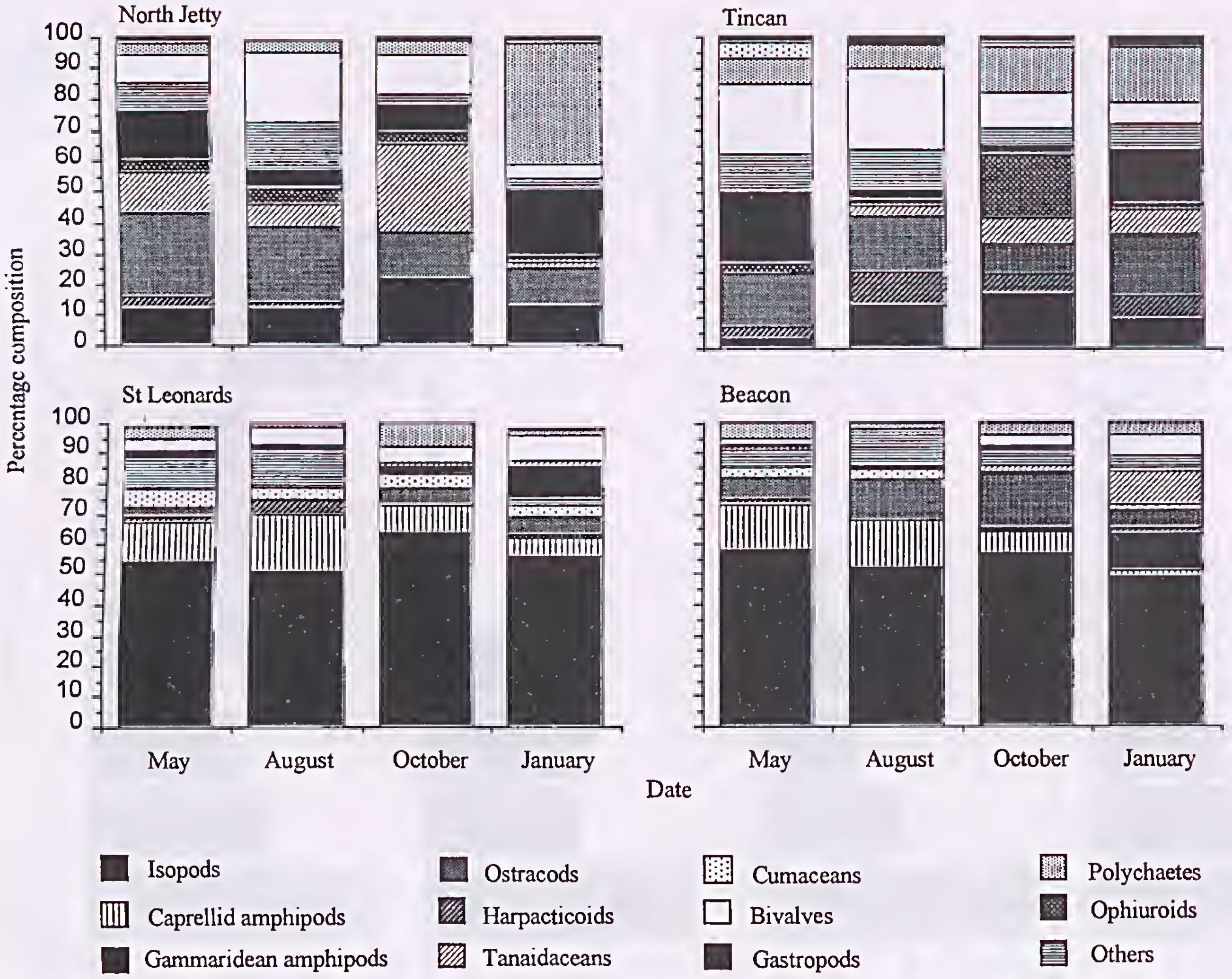

Fig. 5. Per cent composition of macrofaunal assemblages at sites in Swan Bay and Port Phillip Bay.

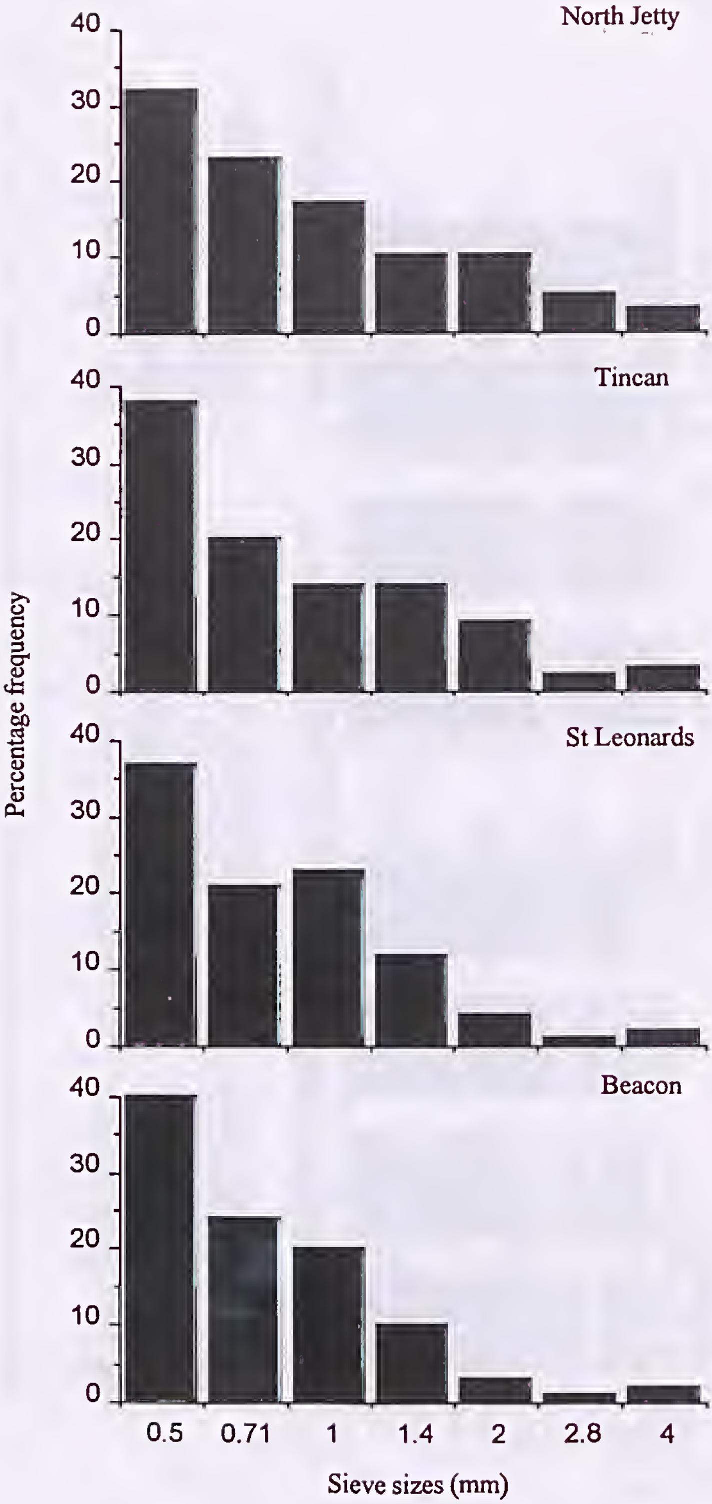

Fig. 6. Per cent frequency of macrofauna in sieve-size classes at sites in Swan Bay and Port Phillip Bay.

least three times more abundant. Cumaceans were also more abundant in Port Phillip Bay. Other invertebrates such as tanaids, gastropods and bivalves were more important at sites in Swan Bay. The January samples from Beacon were unusual in the high representation of tanaidaceans and isopods (Fig. 5). The October samples from Tin Can had unusually high numbers of ophiuroids (Fig. 5).

The size structure of the macrofaunal assemblages showed some variation amongst sites (Fig. 6). Swan Bay sites generally had a higher proportion of larger invertebrates (greater than 1.4 mm sieve size). Port Phillip Bay sites appeared to have a higher proportion of invertebrates in the 1 mm sieve-size class.

Source	Mean square	DF	F-ratio	P
Bay	101.2	1	21.463	0.010
SB sites	6.0	2	2.006	0.142
PPB sites	3.4	2	1.289	0.311
Error	2.6	16		

Table 7. Nested analysis of variance comparing the abundance of meiofauna in Swan Bay (SB) and an adjacent area of Port Phillip Bay (PPB). DF—degrees of freedom; P—probability.

In contrast to macrofauna, abundance of meiofauna was significantly higher in Swan Bay (Table 7). On average, meiofaunal abundance in Swan Bay was approximately four-fold that on the adjacent coast of Port Phillip Bay (Fig. 7). The major difference in the meiofaunal abundances between the two areas occurred in the 0.063 to 0.18 mm sieve-size range (Fig. 8). This was due to the presence of high abundances of epibenthic harpacticoid copepods in this size range in Swan Bay (Fig. 8).

DISCUSSION

Seagrass biomass and organic matter are two physical parameters known to be correlated with invertebrate abundance and diversity in seagrass beds. Heck & Whetstone (1977) found that invertebrate species number and abundance increased with plant biomass. Mann (1988) suggested that organic matter trapped in a seagrass bed would provide food for detritovores and Edgar (1990a) showed that organic enrichment of sediments increased invertebrate production. Edgar & Shaw (1993) found organic matter to be greater in sheltered seagrass beds than unsheltered beds, and this correlated with a higher production of invertebrates in the sheltered environments. Seagrass biomass in Swan Bay and Port Phillip Bay did not significantly differ, but the organic content of sediment was higher in Swan Bay.

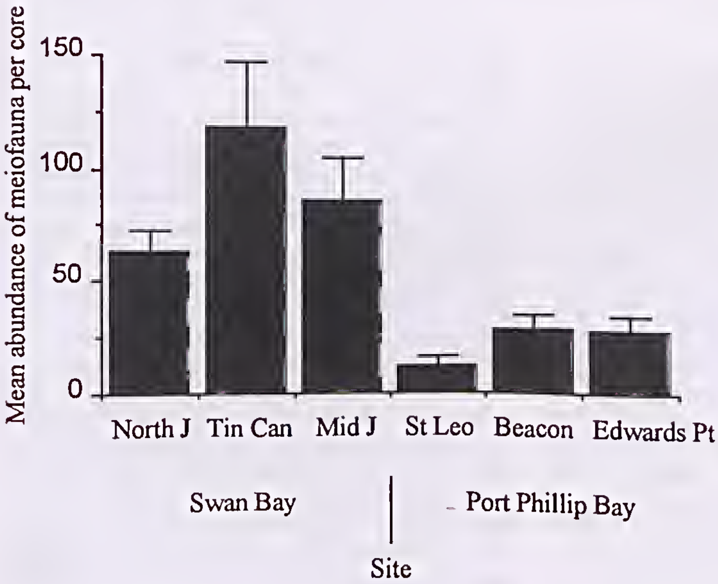

Fig. 7. Mean abundance of meiofaunal organisms at sites in Swan Bay and Port Phillip Bay on 29 October 1990. Error bars are standard error.

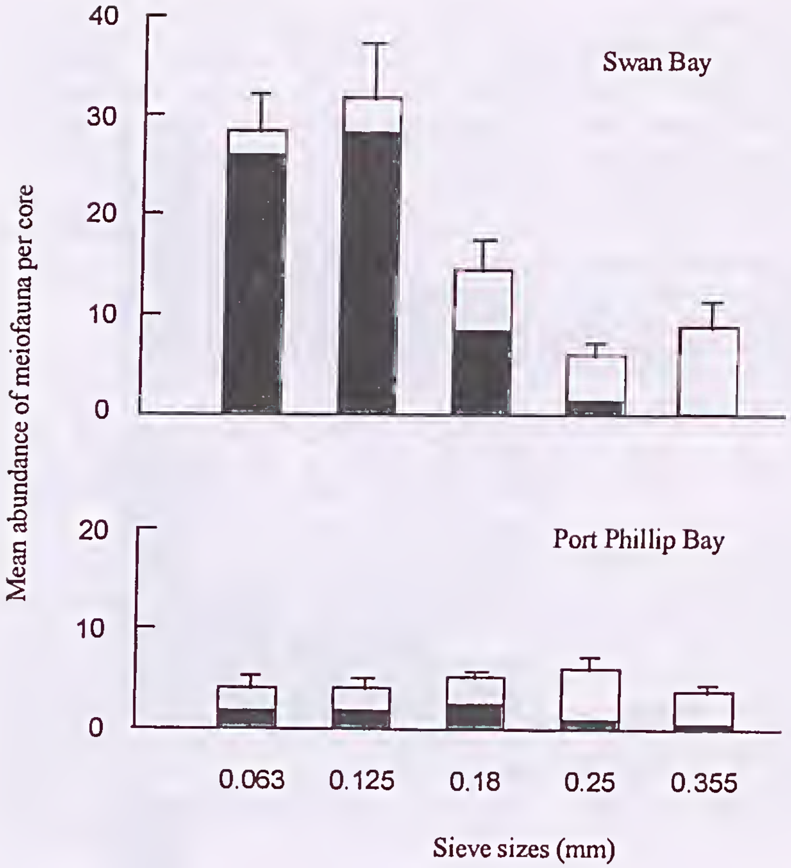

Fig. 8. Mean abundance of meiofauna of different sieve-size components in Swan Bay and Port Phillip Bay. Solid region denotes mean abundance of epibenthic harpacticoids. Error bars are standard error.

Drift algae was seen to accumulate and decompose in Swan Bay and this would enhance organic content of the sediment.

The macrofaunal communities of the two bays were distinctly different. The macrofaunal assemblages at Port Phillip Bay sites were dominated by amphipods, whereas the Swan Bay sites supported a wider range of invertebrate types. The dominance of amphipods in Port Phillip Bay may have been due to the greater exposure to wave action and currents compared with Swan Bay. Fenwick (1976) found that fauna in an algal community was influenced by wave exposure; with a high energy environment characterised by low species diversity and very high densities of amphipods. This distribution is consistent with the suggestion that animals with strong grasping appendages, such as amphipods, often dominate algal communities at exposed sites (Takeuchi et al. 1987; Hagerman 1966). The secure hold an individual has on a blade of seagrass would protect it from the direct effect of wave and current stress.

Macrofaunal abundance gave little indication of the differences between the bays, but Swan Bay had a significantly higher biomass and estimated production of macrofauna than the adjacent area of Port Phillip Bay. This difference was probably because larger invertebrates, especially tanaids and molluscs, were more abundant inside Swan Bay than Port Phillip Bay, thus contributing more to the total biomass and production. Temperature would appear not to have been an important factor influencing production. The highest production estimates for Swan Bay were recorded in May when temperatures were lower than in Port Phillip Bay. High temperatures in Swan Bay over summer may have had a negative effect on epifaunal production by causing migration to deeper water. Differences in macrofaunal production estimated here may be underestimates if there is a difference in the available food resources in the two areas. The equations of Edgar (1990b) were derived from a large number of field studies and would probably have included situations with varying degrees of food limitation. Food limitation in Port Phillip Bay relative to Swan Bay may be important, given the lower organic content of sediments in Port Phillip Bay, and the probable link between organic enrichment and food availability to invertebrates (Edgar 1990a).

Edgar et al. (1994) estimated epifaunal production in seagrass habitats in Westernport Bay to be 17.2 $g.m^{-2}.yr^{-1}$. This value was comparable with macrofaunal production in Port Phillip Bay which ranged between 18.6 and 21.2 $g.m^{-2}.yr^{-1}$. Swan Bay had much higher macrofaunal production levels, ranging between 39.7 and 45.5 $g.m^{-2}.yr^{-1}$. Sites sampled in Westernport Bay by Edgar et al. (1994) would have been closest to our Port Phillip Bay sites in terms of exposure to waves and currents. Our estimates would have been conservative because production estimates did not include animals larger than 5.4 mm sieve size.

Our results concur with those of Edgar & Shaw (1993), who found benthic invertebrate and fish production to be highest in sheltered environments with relatively high organic content of sediments. Organic content was probably higher in Swan Bay due to seagrass debris decaying *in situ* within beds, in contrast to the adjacent area of Port Phillip Bay where wave action would have resuspended debris which could then be transported away by tidal currents. Apart from organically enriched sediment providing increased food resources for deposit feeders (Pearson & Rosenberg 1978; Mann 1988; Spies et al. 1988), sheltered habitats with associated large surface areas of debris and stability of sediments may allow increased colonisation of periphyton food for invertebrates (Edgar & Shaw 1993).

The major difference in the invertebrate communities of the two areas occurs in the meiofaunal size range. The fact that this difference is mainly related to much higher abundances of epibenthic harpacticoid copepods is of great significance to the distribution and abundance of juvenile fish. These copepods are typically the dominant prey item of juvenile benthic fish (Feller & Kaczynski 1975; Alheit & Scheibel 1982; Hicks & Coull 1983; De Morais & Bodiou 1984; Gee 1987). Epibenthic harpacticoids were important prey items of many fish species in Swan Bay and the adjacent area of Port Phillip Bay over the period of this study (Bird 1990), and were the dominant prey of newly settled juveniles of the commercially important King George whiting in Swan Bay (Jenkins et al. 1993a). Patterns of distribution of epibenthic harpacticoid copepods found in seagrass in the present study are very similar to those found for this group on intertidal unvegetated sediments of Swan Bay and the adjacent area of Port Phillip Bay (Shaw & Jenkins 1992). Epibenthic harpacticoids were the dominant prey of post-settlement flounder, with the result that feeding (Shaw & Jenkins 1992) and growth (Jenkins et al. 1993b) rates were significantly higher in Swan Bay.

In conclusion, the greater shelter and correspondingly higher organic enrichment of sediments in Swan Bay is associated with increased production of invertebrates, particularly in the meiofaunal size-range, compared to the more exposed coast of Port Phillip Bay. The major difference in distribution of epibenthic harpacticoid copepods, a dominant prey item for young fish, may have a significant influence on the distribution and abundance of juvenile fishes through differential habitat selection and post-settlement survival.

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